

Comparative flight behavior of *Diabrotica virgifera virgifera* and *Diabrotica barberi* in the laboratory

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Abstract

A tethered flight system was used to characterize and compare the flight behavior of western, *Diabrotica virgifera virgifera* LeConte (WCR), and northern, *Diabrotica barberi* (Smith and Lawrence) (NCR), corn rootworms in the laboratory. Distributions of flight durations were skewed towards short flights for both species regardless of sex or age and there was high variability in flight durations and frequency in individual beetles. Flight distributions for WCR were distinctly bimodal, reflecting a dichotomy between short trivial flights and much longer sustained flights. Trivial flight performance did not vary with age but did differ between species. In comparison to WCR, NCR took shorter flights but had a higher frequency of flights over a 23-h period. Overall, WCR beetles logged substantially more flight time in the same period of time. The proportion of individual WCR undertaking sustained flight was relatively low (<24%) and, for females, declined along with sustained flight durations as a function of age. Periodicity of trivial flight did not differ between the species. In general, flight activity was greatest during early morning and early evening hours. No correlations were found between any feature of flight performance and body size or wing loading ratios.

Introduction

Dispersal is a key process in the population dynamics of many pest insects and is now recognized as an important feature in the life histories of two of the most important corn rootworm species, *Diabrotica virgifera virgifera* LeConte, the western corn rootworm (WCR); and *Diabrotica barberi* (Smith and Lawrence), the northern corn rootworm (NCR) (Cinereski & Chiang, 1968; Haddock, 1984; Coats *et al.*, 1986; Naranjo & Sawyer, 1989; Grant & Seevers, 1989). Both species are major pests of corn, *Zea mays* L., throughout much of the U.S.A. where, as larvae,

they inhabit the soil and feed on the roots of corn. For pest management, the two species are rarely differentiated despite distinct differences in features of their biology and ecology including adult feeding habits, reproduction, and patterns of dispersal (Ludwig & Hill, 1975; Hill & Mayo, 1980; Branson & Krysan, 1981; Naranjo & Sawyer, 1987).

More effective management of corn rootworms depends on a better understanding of the important differences between the species. With growing interest in management strategies focusing on the adult beetle, as opposed to larvae, an understanding of differences in dispersal strategies

between the species is critical. Available evidence suggests that WCR beetles engage in migratory flights as pre-ovipositional females that may take them considerable distances from fields in which they emerged (Coats *et al.*, 1986; Grant & Seevers, 1989); however, they are rarely found feeding outside cornfields (Ludwig & Hill, 1975; Hill & Mayo, 1980). Movement of NCR appears to be localized and more closely related to features of habitat quality, in particular seasonal changes in corn phenology (Haddock, 1984; Naranjo & Sawyer, 1988; Lance *et al.*, 1989). Adult NCR frequently venture from cornfields where they feed on a variety of flowering plants (Cinereski & Chiang, 1968; Ludwig & Hill, 1975; Hill & Mayo, 1980). This study was undertaken to examine and compare the flight behavior of WCR and NCR beetles under controlled laboratory conditions utilizing a computer-interfaced, tethered flight system.

Methods and materials

Insect sources. Adult WCR beetles were reared from eggs of adults collected near Mead, Nebraska, U.S.A. in the late summer of 1987. Adult NCR were reared from eggs of adults collected in Brookings County, South Dakota in 1987. Larvae of both species were reared on seedling corn, using an established laboratory protocol (Branson *et al.*, 1988). Adults were provided seedling corn leaves, young corn ears with silk, corn pollen, and water and were maintained at room temperature (22–25 °C) with a L14:D10 photoperiod until assayed for flight performance.

Flight assays. A computer-interfaced tethered flight-device (Wales *et al.*, 1985; Barfield *et al.*, 1988) was used to examine and quantify the flight behavior of both species. The device is designed so that the insect flies in a vertical plane and rests on a substrate when not flying. Briefly, the insect is tethered to the end of a balanced, lightweight lever which pivots on a fulcrum and has a small flag attached to the opposite end. The flag breaks (insect resting) or does not break (insect flying) an

infrared beam that generates an electrical signal that is then interpreted by the computer. The flight-device, which was originally designed for noctuid moths, was modified slightly to accommodate the relatively small size of the beetles examined here. Also, activity sensors (infrared emitter-detectors) were shielded so that flight activity could be evaluated with a photoperiod and the oviposition drum from the original flight-device was not used. The device has 24 individual actographs, which are contained within vented boxes (4 actographs per box) constructed of plexiglass and wood with a hinged door. The flight-device is housed in two walk-in environmental chambers (12 actographs per chamber), maintained at 25 ± 1 °C and $60 \pm 10\%$ r h with a L14:D10 photoperiod. Technical aspects of design and operation of the flight-device are detailed in Wales *et al.* (1985) and Barfield *et al.* (1988).

Beetles to be flown were anesthetized with CO₂ and were tethered (by the pronotum) with dental wax to the end of a length of quilting thread, the other end of which was connected to a small copper tube (10 mm by 1 mm I.D.), which then fit over the end of the lever described above. Individual beetles were exposed to CO₂ for less than 1 min. Beetles were flown for 23 h beginning 1200–1400 h CST. For each beetle, the device recorded the duration of each flight, the clock time of flight initiation and termination, and the total number of flights over the 23-h period. Beetles were not provided with food or water during the assay period.

Flight experiments and statistical analysis. Beetles of both species and sexes from three age groups were assayed: 2–7 days, 10–17 days, and 20–31 days post emergence. Following completion of the assay, female beetles were dissected to determine ovarian stage on a scale of one to four (Cinereski & Chiang, 1968) and to confirm mating status by checking for sperm in the spermatheca. Any unmated females were discarded from the assay. For many of the beetles that flew, additional data were collected on dry body weight and wing area for the purpose of

examining relationships of age and flight performance with morphometric characteristics. Between 50–90 beetles of each species, sex and age group were assayed. The actual number of beetles that flew varied among the 12 test groups. Beetles that died during the 23-h assay period were not included in the analysis. Two means were calculated for each individual for analysis of species differences: one for trivial flight duration and one for sustained flight duration (this distinction is discussed below). Differences between species and age groups were analyzed by the Kruskal-Wallis rank-sum test (Conover, 1980). Spearman's rank correlation was used to examine the relationships of flight performance with body size and wing loading ratios. G-tests (Sokal & Rohlf, 1981) were used to test for differences in the proportion of beetles displaying sustained flight, and to test for differences in daily flight periodicities between the species and sexes. Finally, t-tests were employed for various mean comparisons.

Results

Distributions of flight durations and flight frequencies. Combining data across all age groups, distributions of all individual flight durations and distributions of the longest flight taken by each beetle (inset) are presented in Figs. 1 and 2. Examination of all flights indicated that at the population level distributions were highly skewed with the vast majority of flights lasting less than 1 min for both sexes of both species. Distributions declined exponentially with increasing flight duration and were clearly different between WCR and NCR beetles. Distributions of WCR flights were distinctly bimodal with a sharp demarcation between flights lasting up to 17–18 min and flights lasting 20–30 min or more. In contrast, flights over 9–10 min were extremely rare for either sex of NCR. Examining individual performance, the same general patterns were apparent from distributions of the longest flight made by each beetle

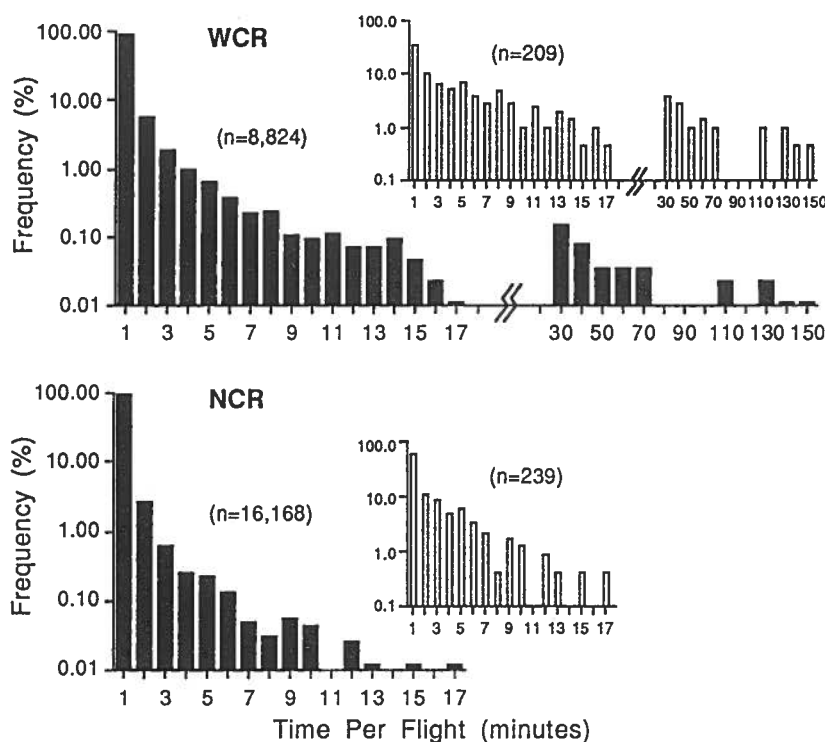


Fig. 1. Distributions of durations of all flights by females of the western corn rootworm (WCR) and the northern corn rootworm (NCR) and distributions of the longest flights by each individual beetle (insets). Note the logarithmic y-axis and the discontinuous x-axis for WCR beetles. Sample sizes are given in parentheses.

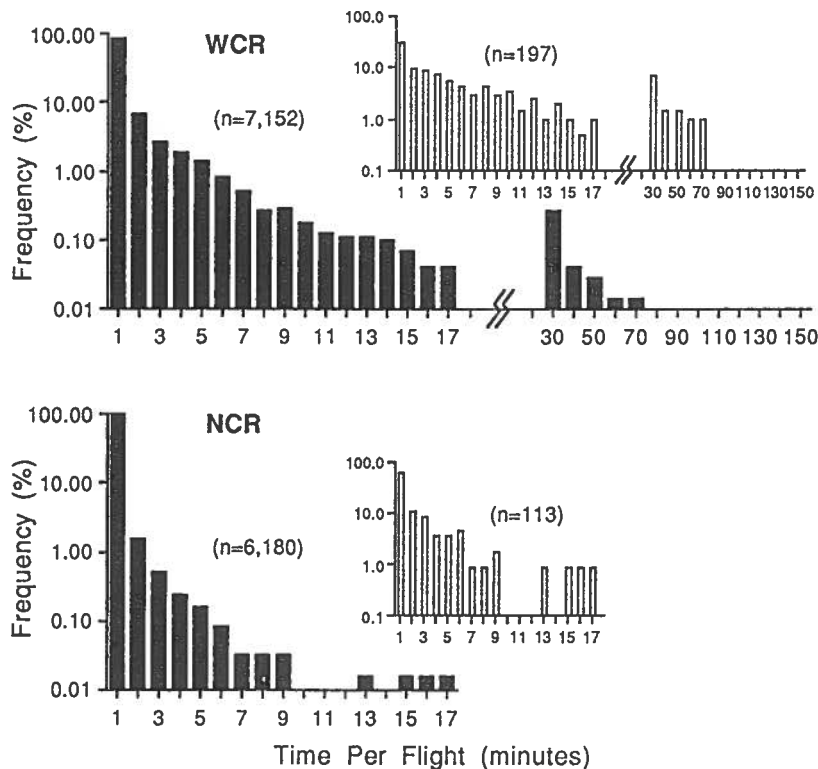


Fig. 2. Distributions of durations of all flights by males of the western corn rootworm (WCR) and the northern corn rootworm (NCR) and distributions of the longest flight by each individual beetle (insets). Note the logarithmic y-axis and the discontinuous x-axis for WCR beetles. Sample sizes are given in parentheses.

(Figs. 1 and 2, insets). The longest flights of the majority of individuals were less than 5 min in duration and distributions declined exponentially with increasing flight duration.

The long flights of WCR beetles have been previously demonstrated (Coats *et al.*, 1986) and most likely represent sustained migratory flight. For further analyses two types of flight were recognized based on observed distributions of flight durations: individual flights < 20 min were considered trivial flights; those lasting ≥ 20 min were considered sustained flights. This differs from the definition of sustained flight used by Coats *et al.* (1986) and others (e.g. Dingle, 1965) who considered sustained flights as those flights lasting > 30 min. The bimodal distributions of flight durations here suggest that, given the tethered flight system used, 20 min is a more appropriate criterion for delineating these two

types of flight in WCR beetles. Based on either criterion, NCR did not exhibit sustained flight.

Data presented in Figs. 1 and 2 demonstrate that there was considerable variation in flight duration at both population and individual levels. There was also considerable variation between individuals in the number of flights taken in the 23-h assay period. Distributions of flight frequency for both species and sexes are presented in Fig. 3. As with flight duration, distributions were skewed towards relatively low frequencies of flight in the majority of individuals and very few individuals taking more than 200–300 flights in a 23-h period. Again, there were noticeable differences in the distributions between WCR and NCR beetles, particularly female NCR, where the distribution tailed out to over 700 flights per beetle. There were no distinct differences between WCR that undertook only trivial flight in com-

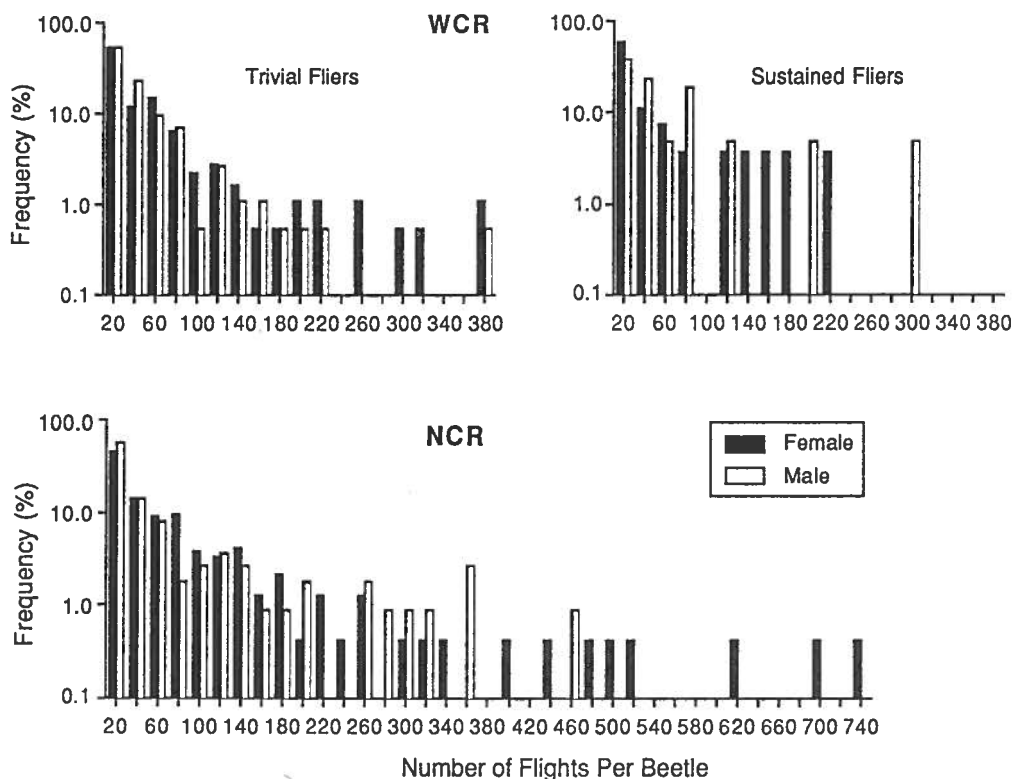


Fig. 3. Distributions of number of flights per beetles (23 h period) for western (WCR) and northern (NCR) corn rootworms. Note the logarithmic y-axis. Trivial flight: WCR female, $n = 181$; WCR male, $n = 179$; NCR female, $n = 239$; NCR male, $n = 113$; Sustained flight: WCR female, $n = 28$; WCR male, $n = 18$.

parison with those that engaged in a least one sustained flight.

While there were discernible differences between the species, on an individual basis, there were few striking patterns to the tremendous variation in flight performance within a species. Although there existed a general positive relationship between flight frequency and the total time an individual spent flying in a 23-h period, there was no relationship between flight frequency and the variance in flight duration within individual beetles. For instance, combining sexes, nearly 40% of all NCR and 27% of all WCR beetles took less than 20 flights all of which were less than 1 min in duration. However, a number of beetles of both species that took less than 20 flights had a combination of very short (< 10 s) and fairly long flights (3–5 min). At the other extreme, about 19% of all NCR and 10% of all WCR beetles

took more than 100 flights in the 23-h assay period. While many of these individuals engaged in flights as long as 10 min others took none greater than 1 min in duration. Even WCR beetles that engaged in at least one sustained flight were, with the exception of this one flight, indistinguishable from those that demonstrated only trivial flight. Some individuals that had sustained flights lasting over 40 min still took well over 100 flights, many of which were as short as 5 s in duration. Still others took only a single long flight lasting over 30 min.

To facilitate comparisons between the species and sexes in the following sections individual flight durations were summarized by calculating a mean flight duration over all flights made by a given individual. Two means were calculated for WCR beetles, one for trivial and one for sustained flight.

Trivial flight behavior. No significant differences were detected in trivial flight performance in relation to beetle age for either sex of WCR or NCR beetles ($P > 0.05$); therefore, further analyses were performed on data pooled across age groups. Results are presented in Fig. 4. All aspects of flight performance were extremely variable between individuals as indicated by differences in the 25th and 75th percentile values.

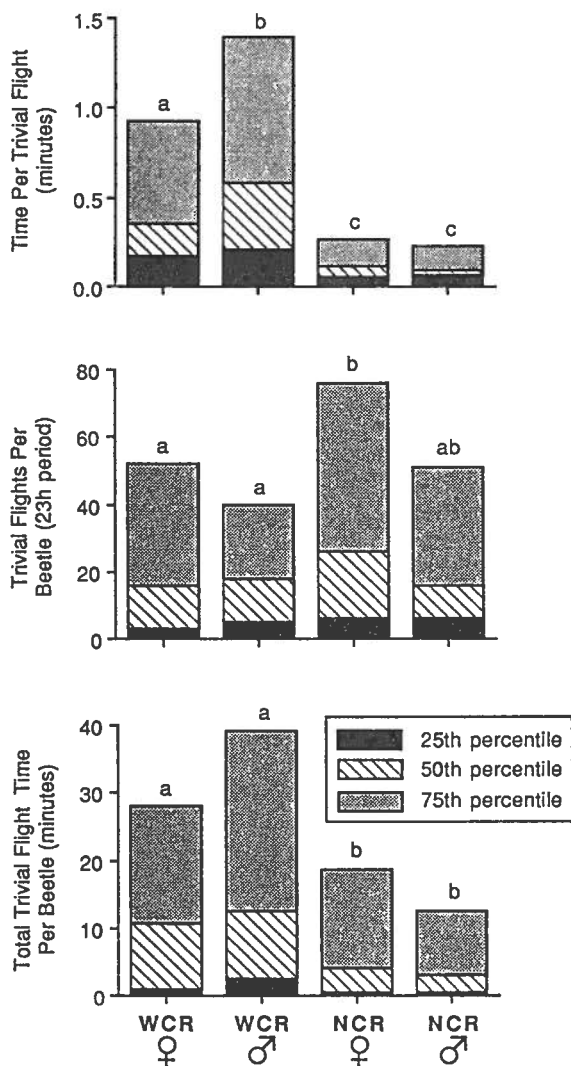


Fig. 4. Trivial (individual flights < 20 min) flight behavior of female and male western corn rootworm (WCR) and northern corn rootworm (NCR) beetles. Bars with different letters are significantly different (Kruskal-Wallis test, $P < 0.05$). WCR female, $n = 209$; WCR male, $n = 197$; NCR female, $n = 239$; NCR male, $n = 113$.

Nonetheless, some interesting patterns emerged. Median flight durations were significantly ($P < 0.05$) greater for WCR in comparison to NCR and significantly ($P < 0.05$) greater for male than female WCR. In general, WCR flights were ca. three and six times longer than NCR flights for females and males, respectively. The frequency of flights over the 23-h assay period followed an opposite trend. Female NCR took significantly ($P < 0.05$) more flights in the same time period as WCR females. There were no significant ($P > 0.05$) differences in flight frequency between WCR females and males and NCR males. The total flight time logged in a 23-h period differed significantly ($P < 0.05$) between the species but not between sexes within a species. In general, WCR beetles flew about 11–12 min over a 23-h period in contrast to NCR beetles, which flew only 3–4 min over the same period of time.

Sustained flight behavior. Sustained flight performance was also quite variable (see Figs. 1 and 2) and, in contrast to trivial flight, there were distinct age effects (Fig. 5). Relatively few of the WCR beetles tested undertook sustained flight, and significantly ($P < 0.05$, G-test) fewer females engaged in sustained flight as they aged. About 24% of females between the ages of 2–7 days undertook sustained flight while only about 4% of females between the ages of 23–30 days undertook sustained flight. It should be noted that 75% of these older females had fully developed ovaries (stage four of Cinereski and Chiang, (1968)). Ovaries of the females in the two younger age classes were much less developed (stages one or two) and were considered pre-ovipositional. Males also displayed sustained flights but the proportion of individuals was lower compared to females and apparently was not influenced by age ($P > 0.05$). Median durations of flight were highest for young females and declined with age. The longest sustained flight, 158.5 min, was logged by a 5-day-old female whereas the longest flight by a male was 54.5 min. Western corn rootworm beetles took only one to two of these sustained flights over a 23-h period and there was little variation within age groups or between sexes.

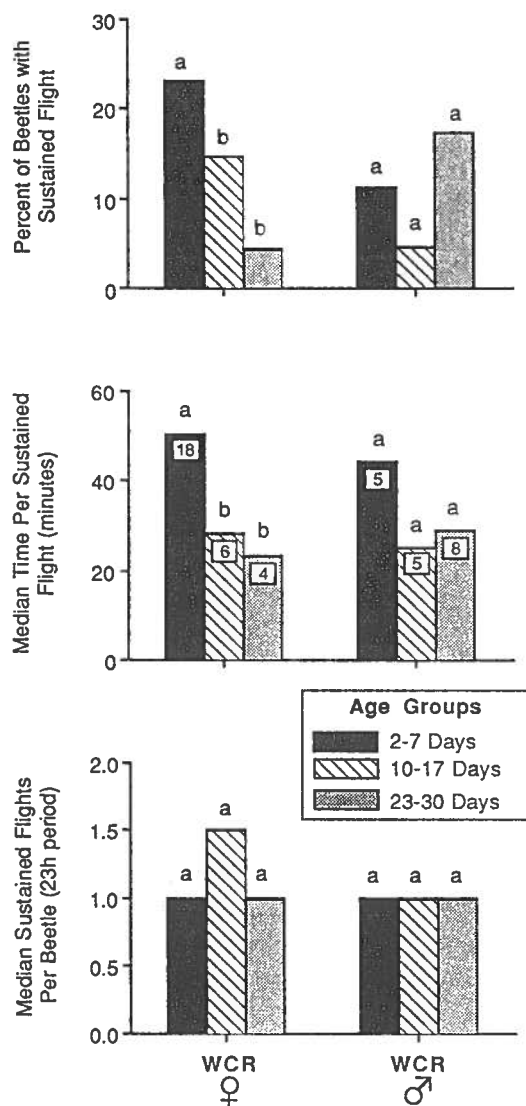


Fig. 5. Sustained (individual flights ≥ 20 min) flight behavior of female and male western corn rootworm (WCR) beetles of different age classes. Bars with different letters within a sex are significantly different (Kruskal-Wallis test, $P < 0.05$). Numbers within bars denote sample sizes.

Body size, wing loading and flight performance. Data on age and flight behavior in relation to reproductive status, body size and wing loading ratios are presented in Table 1. An ovary rating of one indicates undeveloped ovaries and stage four indicates completely developed ovaries with mature chorionated eggs in or ready to enter the oviducts. Due to reproductive development, both

body size and wing loading ratios increased with age in females of both species. For WCR, there were no significant differences in ovarian development between those beetles engaging in only trivial flight and those taking at least one sustained flight ($P > 0.05$, G-test). There was a trend for slightly larger females with higher wing loading ratios to engage in sustained flight; however, none of these differences were statistically significant ($P > 0.05$, t-test) within an age group (Table 1). There were no significant correlations ($P > 0.05$, Spearman's rank correlation) between WCR dry body weight or wing loading and any characteristic of trivial or sustained flight performance, including average flight duration, number of flights, and total flight time.

Comparing the species, NCR had smaller body sizes in all age groups but significantly ($P < 0.05$, t-test) larger wing loading ratios in only the medium aged female group (10–17 days-old) (Table 1). Both males and 23- to 30-day-old female NCR had significantly lower ($P < 0.05$, t-test) wing loading ratios than comparable WCR beetles. Results for younger females may have been due to the slightly higher ovarian ratings for NCR compared to those of WCR. Nonetheless, mature WCR females had almost double the wing loading ratios of mature NCR. Again, there were no significant correlations ($P > 0.05$, Spearman's rank correlation) between NCR body size or wing loading ratios and flight performance.

Daily flight periodicity. Daily periodicities of trivial flight are presented in Fig. 6 for WCR and NCR beetles. Since flight assays were initiated between 1200–1400 h and lasted only 23 h, data for flights between 1100–1300 h are not presented. There appeared to be a peak of activity at 1400 h, particularly for WCR, which is probably related to the propensity for flight soon after tethering. To avoid any bias, the 14 h time period was also eliminated from statistical analysis. In general, the activity of both species was greater during daylight hours with peaks of activity during early morning, late afternoon, and early evening hours. There was little activity during the scotophase. Periodicities of flight activity were not signifi-

Table 1. Summary of age and flight behavior in relation to reproductive status, body size and wing loading

Treatment	Ovarian stage (median)	Mean \pm S.E.		N
		Dry weight (mg)	Wing loading (mg per mm ²)	
<i>WCR:</i>				
2–7 Day Female				
Trivial Fliers	1	2.64 \pm 0.12	0.058 \pm 0.002	40
Sustained Fliers ^a	1	3.17 \pm 0.78	0.071 \pm 0.017	13
10–17 Day Female				
Trivial Fliers	2	3.29 \pm 0.11	0.074 \pm 0.003	35
Sustained Fliers	2	3.54 \pm 0.28	0.079 \pm 0.006	4
23–30 Day Female				
Trivial Fliers	4	5.45 \pm 0.19	0.125 \pm 0.004	35
Sustained Fliers	3.5	6.27 \pm 1.25	0.144 \pm 0.018	3
7–25 Day Males				
Trivial Fliers	–	3.07 \pm 0.05	0.071 \pm 0.001	39
Sustained	–	3.02 \pm 0.16	0.069 \pm 0.003	9
<i>NCR:</i>				
2–7 Day Female	1.5	2.23 \pm 0.09	0.062 \pm 0.002	62
10–17 Day Female	3.5	2.97 \pm 0.07	0.085 \pm 0.002	44
23–30 Day Female	4	3.04 \pm 0.10	0.084 \pm 0.002	56
7–25 Day Male	–	1.95 \pm 0.03	0.058 \pm 0.001	65

^a Beetles that took at least one flight \geq 20 min.

cantly different ($P > 0.05$, G-tests) between the sexes of either species or the species of either sex. Periodicities of sustained flights for WCR were similar to those reported by Coats *et al.* (1986), with activity being confined mainly to early morning and evening hours.

Discussion

The results of this study are qualitatively similar to those of tethered flight studies in other insects (e.g., Johnson, 1976; Davis, 1980) in that the flight behavior both within and between individuals is extremely variable and that distributions of flight durations, viewed on either population or individual levels, were skewed towards relatively short flights. At the population level 96% and 87% of all flights were less than or equal to 1 min for NCR and WCR beetles, respectively. Similarly, the longest single flight by 60.8% and 32.8% of individual NCR and WCR beetles, respec-

tively, were less than 1 min in duration. There was also tremendous variation in flight performance both between and within individual WCR and NCR beetles. A small percentage of WCR beetles engaged in long duration, sustained flights, however, most of these individuals also took short flights lasting less than 1 min. At the opposite extreme many individual WCR and NCR beetles never engaged in any flights longer than 1 min. No discernible patterns in this variation were apparent within either species or even between WCR beetles that display only trivial flight and those engaging in some sustained flight. It remains to be seen if such variability exists in nature and what role it may play in the life history of these beetles.

Overall, it is difficult to determine to what extent the nature of the tethered flight system, and/or the highly artificial conditions of the assays, influenced the qualitative and quantitative features of flight in these species; thus, extrapolation of results to quantify dispersal in the field is problematic. Despite this drawback, the com-

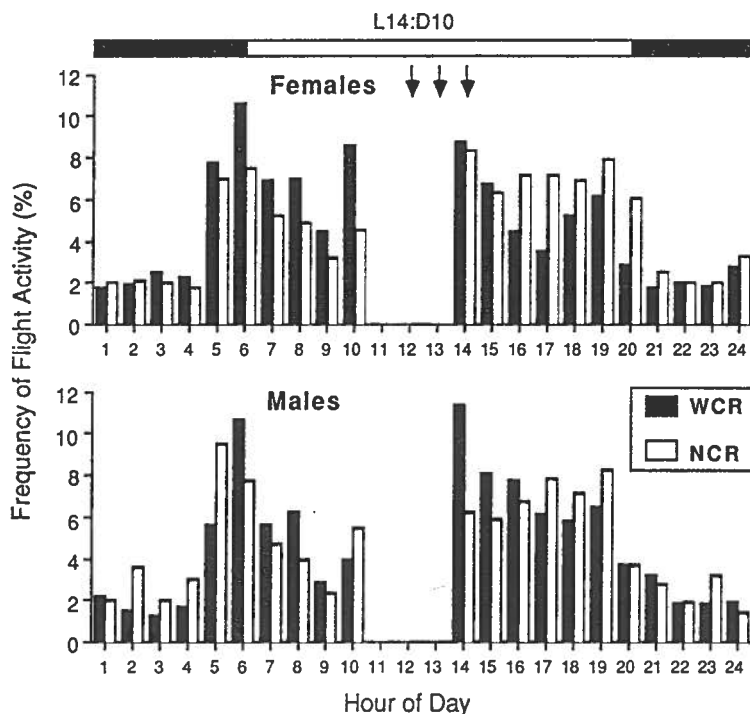


Fig. 6. Comparison of the daily periodicity of trivial (individual flights < 20 minutes) flights by western corn rootworm (WCR) and northern corn rootworm (NCR) beetles. Flights are grouped by the nearest hour of flight initiation. Horizontal bar represents the photoperiod regime; arrows designate the time period over which flight assays were initiated. Data for the hours 1100–1300 are not presented because assays lasted only 23 h. WCR female, $n = 181$; WCR male, $n = 179$; NCR female $n = 239$, NCR male, $n = 113$.

parative patterns of behavior may lend insight into how flight behavior in these insects has been shaped by the differential strategies of dispersal displayed by these beetles in the field. Corn rootworms are generally univoltine (some NCR populations display semivoltinism [Krysan *et al.*, 1986]), are functionally monophagous on corn as larvae, and, due to crop rotation, are faced with spatial variability in host plant availability from season to season. Thus, adult beetles must not only be able to colonize new habitat patches (cornfields) suitable for the development of their progeny but also be able to find sufficient food to ensure survival and permit reproduction. The life history strategies apparently used by the two species to accomplish this goal differ in significant ways.

Adult WCR feed on a broader range of corn tissues, including silks, pollen, and foliage, and

while less inclined to leave cornfields, will do so to locate other feeding and oviposition sites (Hill & Mayo, 1974; Branson & Krysan, 1981). In large part this local dispersal is most likely the result of trivial flight. However, there is compelling evidence of long-distance migratory flight by this beetle, including the expansion of its range from Colorado to the eastern seaboard of the U.S.A. in this century, the ubiquitous presence of populations resistant to cyclodiene pesticides (Metcalf, 1986), and just recently, evidence of beetle movement in relation to synoptic-scale weather patterns (Grant & Seevers, 1989).

This study and the work of Coats *et al.* (1986) clearly demonstrate the capacity for sustained flight necessary for long-distance movement in WCR, although given the ubiquitous presence of corn within the geographic range of WCR, the adaptive value of this capacity is unclear. Further-

more, there is evidence, at least in young females, that sustained flight may be hormonally controlled (Coats *et al.*, 1987). While Coats *et al.* (1986; 1987) did not test females over 15 days of age or males, results here indicate that sustained flight is not restricted to pre-ovipositional females because it was found in gravid females as old as 30 days of age and in males ranging from 7–25 days of age. It should be noted that the definition of sustained flight here (i.e., flights ≥ 20 min. in duration) differed from that of Coats *et al.* (1986). However, as these authors did not observe flight durations in the interval from 17–30 min our definitions of sustained flight are equivalent. Sustained flight in males has been found in other insects (e.g. Dingle, 1965) and may be an adaptive response which would allow individuals to locate females over long distances, particularly if males had failed to mate. Because males in this study were given access to females, it is not known to what degree mating failure might have influenced the propensity for sustained flight. Relatively few of the individuals tested ($< 24\%$) demonstrated sustained flight in any age group, and in general, females were more inclined than males to undertake long flights. Clearly, young females (2–7 days old) exhibited the strongest sustained flight capacity with the greatest percentage of individuals taking flights of the greatest duration (see Fig. 5). As females aged, they were less likely to undertake sustained flight and those that did took flights of significantly lower duration in comparison with young females. Western corn rootworms are, thus, clearly capable of colonizing cornfields at considerable distances from their field of origin, even though a relatively small portion of a given population may do so.

The relationship between reproduction and flight in WCR is unclear. Coats *et al.* (1986; 1987) found that while trivial flight occurred throughout the lifetime of WCR beetles, both trivial and sustained flight activity peaked in 5- to 6-day-old females and sustained flight was inversely related to ovarian development in beetles up to 15 days of age. Although analyses here were restricted to fairly crude age groups, results indicated no significant age-effect on trivial flight behavior in

females up to 30 days of age and representing the entire range of ovarian development. Furthermore, sustained flight, though somewhat diminished, was found in some gravid females and in some males. The extent to which these patterns occur in the field is uncertain; however, data suggest that the oogenesis flight syndrome, as defined by Johnson (1969), and which characterizes the migratory behavior of many insects, may not adequately define the phenomenon in WCR beetles.

In contrast to WCR, NCR feed on only the flowering parts of corn and readily move outside corn to secure other sources of pollen (Cinereski & Chiang, 1968; Ludwig & Hill, 1975), particularly in response to declining food availability in cornfields as they mature (Haddock, 1984; Naranjo & Sawyer, 1988). Based on data collected by Cinereski & Chiang (1968) and Lance *et al.* (1989), movements between corn and non-corn habitats by NCR may be cyclic, with insects alternating between bouts of feeding and oviposition. There is no evidence of long-distance migration by NCR, and high interpopulation genetic variance (McDonald *et al.*, 1985) suggests that movement may be highly localized. The comparatively short but more frequent flights by NCR, in comparison with WCR, may facilitate the hypothesized cyclic nature of their movement between corn and non-corn habitats. Such flights would tend to reduce the net distance travelled and thus insure that beetles remain near corn. The spatial scale of these movements is uncertain; however, since Haddock (1984) trapped NCR beetles in isolated areas over 3 km from cornfields, their movement is great enough to ensure the colonization of new fields, at least on local scales. Once again, based on flight assays, there is no evidence of a relationship between reproduction and flight in this insect. This is further supported by Cinereski & Chiang (1968) who found NCR females in habitats surrounding cornfields and females in cornfield with non-corn pollen in their guts representing all ovarian classes.

Any relationship between size, reproduction and flight is unclear in these two species. Mor-

phometric characteristics were not statistically related to the quantitative features of flight performance in either species. Insects with lower wing loading ratios were no more or less likely to take more flights or undertake flights of longer duration and there were no significant differences in body size or wing loading between trivial and sustained fliers of WCR. Davis (1980) reported a similar lack of correlation between body size and flight performance in tethered flight studies of *Tetraopes tetraophthalmus* (Forster) beetles. Furthermore, wing loading ratios increased significantly with age, but there were no statistical differences in flight performance with increasing age, at least for trivial fliers. There were also no clear patterns in comparing the two species. Western corn rootworm beetles are considerably larger (see Table 1) and clearly have a greater capacity for flight in both sexes, however, mature NCR females have much lower wing loading ratios than mature WCR females and male NCR have lower wing loading ratios than WCR males. Although lower wing loading ratios may permit more energy-efficient flight, particularly in migratory species, there are many trade-offs in the allocation of resources and energy that shape the relationships between body size, flight capacity, and reproduction within and between related species (Angelo & Slansky, 1984). Further study will be needed to unravel these complex relationships in *Diabrotica*. If the simple assumption that wing loading ratios correlate with flight energetics is considered, data here indicate that, all else being equal, flight is energetically more costly to WCR in comparison with NCR.

Dispersal is a key component in the life history of the two species of *Diabrotica* examined here. Ecologically, both species seek to exploit a resource which is discontinuous in both space and time. Diapause in the egg stage partially circumvents the temporal aspect by synchronizing these insects with their seasonally available host plant. Dispersal allows continuity in space. The features of flight behavior which underlie movement of these insects in nature are clearly different and may reflect the divergence in dispersal strategies found in these two species. Responses to

environmental cues such as habitat quality and type will clearly modify basic flight characteristics; however, data suggest that WCR may colonize new habitats at larger spatial resolutions than NCR. Predicting the timing and magnitude of beetle movement within the corn agroecosystem is central to developing strategies for managing adult corn rootworm populations over a wide area. This work highlights the importance of species differences. Further work is needed to extrapolate and quantify these differences, and their consequences, in the field.

Résumé

Comparaison au laboratoire des comportements de vol de Diabrotica virgifera virgifera et D. barberi

Un système de vol captif a été utilisé pour caractériser et comparer au laboratoire les comportements de vol de *D. virgifera virgifera* et *D. barberi*. La distribution des durées de vol est nettement biaisée avec la grande majorité des vols durant moins d'une minute quels que soient le sexe et l'âge. Il y a une grande variabilité interindividuelle tant en durée qu'en fréquence de vol. Les distributions des durées de vol en fonction du sexe sont bimodales chez *D. virgifera virgifera*, mais pas chez *D. barberi*, ce qui reflète la séparation entre vols brefs ordinaires et long vols prolongés. Les vols brefs ordinaires ne dépendent pas beaucoup de l'âge ou du sexe mais diffèrent suivant l'espèce. *D. barberi* a eu des vols plus brefs, mais en a effectué plus pendant une période de 23 heures. Au total, *D. virgifera virgifera* a consacré nettement plus de temps au vol pendant la même période; mais, chez cette espèce la proportion d'individus effectuant des vols soutenus était relativement faible (< 24%), avec une diminution de leur nombre avec l'âge chez les femelles; le nombre le plus élevé étant chez les jeunes femelles. La périodicité des vols ordinaires n'a dépendu ni du sexe, ni de l'espèce; l'activité de vol a été en général plus importante tôt le matin et en début de soirée. Aucune corrélation n'a été trouvée entre une quelconque performance de vol et la taille du corps ou la charge alaire.

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